

Climate change has affected the breeding date of tree swallows throughout North America

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Increasing evidence suggests that climate change has affected the breeding and distribution of wildlife. If such changes are due to global warming, then we should expect to see large-scale effects. To explore for such effects on avian reproduction, we examined 3450 nest records of tree swallows from across North America. The egg-laying date in tree swallows advanced by up to nine days during 1959–1991. This advance in phenology was associated with increasing surface air temperatures at the time of breeding. Our analysis controlled for several potentially confounding variables such as latitude, longitude, breeding density and elevation. We conclude that tree swallows across North America are breeding earlier and that the most likely cause is a long-term increase in spring temperature.

Keywords: timing of reproduction; laying date; *Tachycineta bicolor*; global warming

1. INTRODUCTION

There is growing concern that global warming may alter the distribution, reproduction and life history of plants and animals. For example, long-term studies in Europe have shown that warmer surface air temperatures are associated with a lower body size and condition of ungulates (Post *et al.* 1997), earlier spawning by amphibians (Beebe 1995) and lower frequencies of melanistic forms of beetles (de Jong & Brakefield 1998). Evidence for ecological effects in bird populations is also mounting (Crick *et al.* 1997; Montevecchi & Myers 1997; Winkel & Hudde 1997; McCleery & Perrins 1998; Brown *et al.* 1999; Crick & Sparks 1999). For example, in the UK, 20 species of birds laid their eggs an average of 8.8 days earlier in 1995 than in 1971 (Crick *et al.* 1997). This nine day difference in laying date is similar to the six to eight day earlier growing season of plants in northern latitudes (Keeling *et al.* 1996; Myneni *et al.* 1997). If global warming is changing the breeding phenology of animal populations, then we might expect to see similar trends in bird populations elsewhere. However, to date the only long-term studies of the effects of climate change on vertebrates outside of Europe have been the local studies of northern gannets (*Morus bassanus*) on Funk Island, Newfoundland (Montevecchi & Myers 1997) and Mexican jays (*Aphelocoma ultramarina*) in south-eastern Arizona (Brown *et al.* 1999). Recent studies have also suggested that climatic change may not act uniformly on all aspects of reproduction nor across the full extent of a species' range (Visser *et al.* 1998; Harrington *et al.* 1999). Thus, continental-scale effects of climate change on wildlife remain to be demonstrated. Here we present the first evidence that increasing surface air temperatures are advancing avian reproductive patterns across an entire continent.

We examined the long-term variation in the laying date of tree swallows (*Tachycineta bicolor*) to examine their breeding phenology in relation to surface air temperature and climate change. Tree swallows are a common and widespread species in the northern USA and Canada. They are mostly monogamous, aerial insectivores that use secondary cavities in trees as nest sites, though they readily accept nest-boxes as alternatives to natural cavities (Robertson *et al.* 1992). As a consequence of their wide geographical range and readiness to use nest-boxes, tree swallows provide one of the largest broad-scale data sets in North America for examining the effects of climate change.

2. METHODS

We examined 40 years (1952–1992) of data from over 21000 nest record cards supplied primarily by the North American Nest Record Card Program (Cornell Laboratory of Ornithology, 1970–1992), British Columbia Nest Records Scheme (BC Wildlife Branch, 1952–1991), Ellis Bird Farm (Lacombe, Alberta, 1981–1986), Maritimes Nest Records Scheme (Canadian Wildlife Service, 1962–1990), Prairie Nest Records Scheme (Manitoba Museum of Man and Nature, 1958–1986) and Quebec Nest Records Scheme (National Museum of Canada, 1959–1988).

All the records used in this study came from nest-boxes, so it is unlikely that any temporal changes were due to differences in nest-site selection. In addition, tree swallows are single brooded (Robertson *et al.* 1992), so our results are not influenced by reports for second broods. We used only records with at least two visits to the nest, including one during laying (typically mid-May to early June). Visits during laying were identified by an increase in the number of eggs on subsequent visits. The laying date (date of clutch initiation) was estimated to within one day by backdating one egg per day from the date of the first record of eggs in the nest. We did not use records from re-nests or from clutches with fewer than three eggs ($n = 43$ clutches) or

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more than eight eggs ($n=26$), because these nesting attempts may have been abandoned early or produced by two females nesting in the same nest-box, respectively.

Our final data set included 3450 clutches from 1959 to 1991. Years with fewer than five nest records (1952, 1955–1958, 1960, 1964–1965 and 1992) were eliminated. The mean number of nests per year was 115 (range = 6–280; all but five years had $n > 20$). These records span most of the normal breeding range of tree swallows across the northern USA and Canada: from California and North Carolina (33–35° N) north to Yellowknife, North-West Territories (63° N), and from Nova Scotia (64° W) west to Oregon and British Columbia (123° W). No data were available from the species' range in Newfoundland and Alaska. Most data came from the Canadian prairie provinces and the Great Lakes region.

Surface air temperatures during breeding were compiled for each clutch in the year and the location where it was laid. Mean monthly temperatures prior to and during laying (April–June) were estimated for each year and 1° block of latitude and longitude (latilong) for which we had nesting data. Mean monthly temperatures (typically 1.5 m above ground) and elevations were compiled from all stations within a latilong block from the Global Historical Climatology Network, v. 2 (Peterson & Vose 1997). On average, data were available from 2.4 weather stations within each yearly latilong.

Laying date could be influenced by a variety of factors. Latitude and longitude were included as predictors to measure geographical effects on laying date and to control for the uneven distribution of our data across the continent. Laying may be delayed in areas of higher swallow density if competition leads to less food per individual, or laying may be earlier if individuals congregate in areas of high food abundance where competition for food is relatively weak. To control for these possibilities, we estimated the density of tree swallows using abundance indices from the Breeding Bird Survey programme of the US Fish and Wildlife Service (Price *et al.* 1995). The mean density values of swallows were calculated for each latilong block using the means of multiple surveys and years where available (mean per block = 4.3 routes and 76.7 total survey years). Individual females differ in quality, which is reflected in part in their clutch size (Winkler & Allen 1996); thus, we also included clutch size as a predictor in our model, even though it is usually thought of as a consequence, rather than a predictor, of laying date.

3. RESULTS

As in other studies, surface air temperatures during 1959–1991 have increased ($r^2=0.45$, $p < 0.0001$). Associated with this advance in temperature, laying date of tree swallows advanced by five days from 1959 to 1991 when we examined all clutches ($r^2=0.01$, $n=3450$ clutches and $p < 0.0001$) and by nine days when we examined the yearly means ($r^2=0.41$, $n=30$ years and $p=0.0001$; figure 1a). Laying occurs in May in most of the range of tree swallows; in our data set the mean (\pm s.e.) of the yearly mean laying dates was 30 May (± 0.75 days and range of yearly means = 21 May–7 June). The laying date was later when the mean monthly temperatures were lower in May ($r^2=0.75$; figure 1b), as well as April ($r^2=0.34$) and June ($r^2=0.24$; analyses of yearly means, all $p < 0.01$).

The advancement in laying date has not been consistent over time. Most of the advancement occurred during the 1960s (2.9 days) and 1980s (3.3 days), while there was

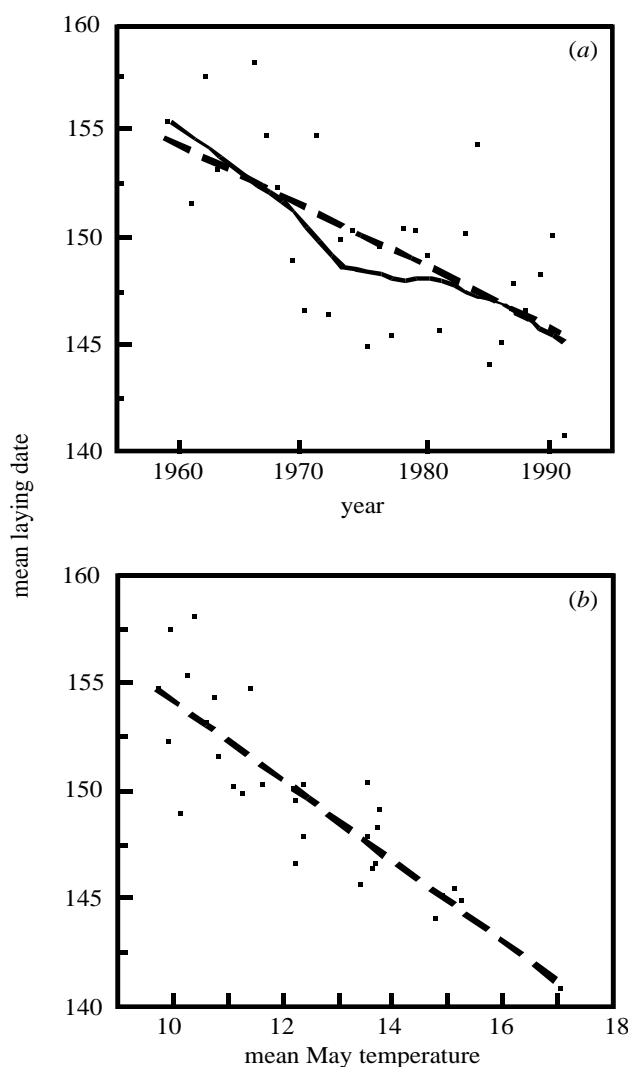


Figure 1. (a) Change in mean laying date (in Julian days) from 1959 to 1991 ($r^2=0.41$, $n=30$ years, $p=0.0001$). (b) Influence of mean May temperature on laying date ($r^2=0.75$, $n=30$ years, $p < 0.0001$). Dashed lines are from linear regressions, and curve is from a LOWESS (locally weighted scatter plot smoothing, tension = 0.5; Wilkinson 1992).

little change during the 1970s (0.5 days) (based on three separate regressions for each decade; see figure 1a). These laying date estimates are potentially influenced by averaging samples of different sizes within each year. However, analysis of the 3450 individual clutches revealed a similar pattern. When individual clutches were analysed based on the three decades above, we again found that there was a greater advancement in laying date during the 1960s (slope \pm s.e. = -0.70 ± 0.20 and $n=137$) and 1980s (slope \pm s.e. = -0.25 ± 0.09 and $n=2042$) than during the 1970s (slope \pm s.e. = 0.33 ± 0.10 and $n=1212$; ANCOVA of laying date on year, decade and their interaction $F_{1,3387}=8.6$ and $p=0.003$).

The interpretation of the causes of these changes in laying date is handicapped by the non-independence of nests measured in the same area and in the same year, where variation in these random effects could bias the interpretation of the data. Spatial and temporal factors could also have

Table 1. *Estimates of fixed effects of each of the potential causes of variation in laying date across North America*

(The degrees of freedom for the intercept were 23, for all other tests they were 2761. Statistically significant effects are indicated by an asterisk.)

effect	estimate	<i>t</i>	<i>p</i>
intercept	144.28	0.99	0.332
year	0.02	0.29	0.775
clutch size*	-2.55	-15.64	< 0.001
elevation	< -0.01	-0.71	0.444
tree swallow density*	-0.08	-2.79	0.005
latitude	-0.55	-1.34	0.180
longitude*	0.21	1.97	0.048
spring temperature*	-3.49	-2.76	0.006
latitude × spring temperature*	0.08	2.64	0.008
longitude × spring temperature*	-0.02	-2.41	0.016

direct fixed effects on laying date variation. To control for the confounding influence of random effects as well as the potential fixed effects of year, latitude and longitude, we used the MIXED procedure in SAS (Littell *et al.* 1996). In this analysis, we analysed the random temporal and spatial effects by including year and latilong block as random effects, both of which had highly significant ($p < 0.001$) effects. We also sought the linear effects of year, latitude and longitude by treating them as fixed effects, along with other predictors, in the same analysis (for a similar application using a temporal variable as both fixed and random effects see Littell *et al.* (1996, p. 117)).

Once the random effects of year were removed, there was no directional effect of year on laying date ($p = 0.77$; table 1). Thus, year had no unmeasured causative variation associated with the advance in laying date, and changes in laying date appeared to be well explained by the other predictors in our model. In particular, the mixed model analysis revealed a strong negative relationship between laying date and spring temperatures (i.e. the mean of April and May temperatures; $p = 0.0001$; table 1), as expected if temperature affects laying date. Swallow density, clutch size and the interactions between temperature and longitude or latitude were also related to laying date (table 1). Interestingly, laying was earlier where tree swallow density was higher ($p = 0.005$), suggesting an aggregation of swallows in areas of high food rather than local competition for food. Similar results were found when we used the density of all species of swallows in these analyses (not shown). Earlier laying was also associated with larger clutch sizes ($p = 0.0001$) and more eastern locations (longitude effect, $p = 0.048$).

Although swallows have been laying earlier throughout their range, the rate of change in laying date has differed geographically. There was a significant negative interaction between longitude and temperature (table 1), which indicates that the relationship between laying date and temperature was steeper (i.e. more negative), and thus the rate of change in laying date was greater, at more western locations (higher longitude). In contrast, there was a positive interaction between latitude and temperature (table 1), which indicates that the relationship between laying date and temperature was steeper, and thus the rate of change in laying date was greater, at more southern locations (lower latitude) within the range of swallows.

4. DISCUSSION

During 1959–1991 tree swallows started breeding earlier by nine days (figure 1), which is consistent with advances in the phenology of vegetation in the north (Keeling *et al.* 1996; Myneni *et al.* 1997; Menzel & Fabian 1999). Studies of growing seasons since 1960 have suggested that most of this change has occurred recently (i.e. 1981–1990; Keeling *et al.* 1996) and at higher latitudes ($> 35^\circ \text{N}$; Myneni *et al.* 1997). Similarly, most tree swallows breed above 35°N and the advancement of their laying date was stronger during the 1980s than the 1970s (figure 1). Overall, tree swallows across the northern United States and Canada are breeding earlier, providing support for a large-scale influence such as global warming.

Other factors besides climate change may be responsible for the shift towards earlier breeding in birds. For example, in declining populations there may be less competition for resources and, as a result, the mean time of breeding in the population may advance. Contrary to expectations, in our mixed model analysis we found that tree swallows actually bred earlier in locations with more individuals (see tree swallow density, table 1), presumably because these birds are proficient at congregating in regions where food availability is highest. We believe these density effects are thus a result of the birds' behavioural adjustment of their distributions and not a causal effect of density on the birds. Thus, while it is true that tree swallows increased during 1966–1993 across North America (Price *et al.* 1995, p. 332), it is difficult to accept that earlier laying could have been a spurious consequence of an increase in density. Similarly, shifts in sampling effort over time could also lead to changes in laying date (e.g. more nest record cards in later years may have come from southern locations where breeding is earlier and the density is higher). However, our analyses showed that the earlier laying dates are strongly inversely related to air temperature, (which increased during the 30 years of this study), even after controlling for latitude, longitude, density and elevation. Thus, we conclude that the most likely and ecologically reasonable cause of the advance in laying date is a long-term increase in spring temperature.

The mechanism for earlier laying in tree swallows is probably an advancement in the date of emergence or peak abundance of aerial insects. Tree swallows feed

primarily on dipterans and other flying arthropods (Robertson *et al.* 1992) whose abundance is directly related to air temperature (Roeder 1953). As a result, the timing of laying by swallows is closely correlated with the abundance of flying arthropods (Winkler & Allen 1996; D. W. Winkler and P. O. Dunn, unpublished data). Timing of breeding is related to the abundance of aerial arthropods in at least 20 other bird species that are aerial insectivores (Robins 1970). Alternatively, higher spring temperatures could advance laying directly by reducing the energy requirements of pre-reproductive females (e.g. Dhondt & Eyckerman 1979).

There are several possible consequences of changes in laying date for tree swallows and other species. In many birds, laying earlier is associated with larger clutch size and more young fledged (Lack 1968; Price & Liou 1989). Indeed, in tree swallows individuals which lay earlier have larger clutches and fledge more young (DeSteven 1978; Stutchbury & Robertson 1988; Winkler & Allen 1996) and their young also have a higher probability of survival (D. W. Winkler, unpublished data). Thus, warmer temperatures might lead to a greater production of young. However, recent evidence from great tits (*Parus major*) has suggested that warmer spring temperatures can lead to a mismatch in the timing of egg laying relative to the availability of food for nestlings and, as a result, later laying females may produce fewer surviving young (Visser *et al.* 1998). Thus, further study is needed of both the precise mechanisms and demographic consequences of climate change (see also Montevecchi & Myers 1997; Harrington *et al.* 1999).

Our study provides an example of how volunteers can provide important data for long-term and large-scale ecological questions (see also Root 1988; Price *et al.* 1995; Harrington *et al.* 1999). Analysis of nest record card data from other species is necessary for ascertaining the generality of the patterns we have found for tree swallows. However, further progress will depend on the contributions of volunteers and the cooperation of nest record programmes throughout North America. We encourage people to contribute additional nest record data to these programmes (see the Acknowledgements), as surface air temperatures are expected to continue to increase (see also Crick & Sparks 1999) and, thus, we expect further advances in the laying dates of tree swallows and other species.

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REFERENCES

- Beebe, T. J. C. 1995 Amphibian breeding and climate. *Nature* **374**, 219–220.
- Brown, J. L., Li, S. H. & Bhagabati, N. 1999 Long-term trend toward earlier breeding in an American bird: a response to global warming? *Proc. Natl Acad. Sci. USA* **96**, 5565–5569.
- Crick, H. Q. P. & Sparks, T. H. 1999 Climate change related to egg-laying trends. *Nature* **399**, 423–424.
- Crick, H. Q. P., Dudley, C., Glue, D. E. & Thomson, D. L. 1997 UK birds are laying eggs earlier. *Nature* **388**, 526.
- de Jong, P. W. & Brakefield, P. M. 1998 Climate and change in clines for melanism in the two-spot ladybird, *Adalia bipunctata* (Coleoptera: Coccinellidae). *Proc. R. Soc. Lond. B* **265**, 39–43.
- DeSteven, D. 1978 The influence of age on the breeding biology of the tree swallow, *Iridoprocne bicolor*. *Ibis* **120**, 516–523.
- Dhondt, A. A. & Eyckerman, R. 1979 Temperature and date of laying by tits *Parus* spp. *Ibis* **121**, 329–331.
- Harrington, R., Woiwod, I. & Sparks, T. 1999 Climate change and trophic interactions. *Trends Ecol. Evol.* **14**, 146–150.
- Keeling, C. D., Chin, J. F. S. & Whorf, T. P. 1996 Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature* **382**, 146–149.
- Lack, D. 1968 Ecological adaptations for breeding in birds. London: Methuen.
- Littell, R. C., Milliken, G. A., Stroup, W. W. & Wolfinger, R. D. 1996 *SAS system for mixed models*. Cary, NC: SAS Institute.
- McCleery, R. H. & Perrins, C. M. 1998 . . . temperature and egg-laying trends. *Nature* **391**, 30–31.
- Menzel, A. & Fabian, P. 1999 Growing season extended in Europe. *Nature* **397**, 659.
- Montevecchi, W. A. & Myers, R. A. 1997 Centurial and decadal oceanographic influences on changes in northern gannet populations and diets in the northwest Atlantic: implications for climate change. *ICES J. Mar. Sci.* **54**, 608–614.
- Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G. & Nemani, R. R. 1997 Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**, 698–702.
- Peterson, T. C. & Vose, R. S. 1997 An overview of the Global Historical Climatology Network temperature data base. *Bull. Am. Meteorol. Soc.* **78**, 2837–2849.
- Post, E., Stenseth, N. C. & Fromentin, J. M. 1997 Global climate change and phenotypic variation among red deer cohorts. *Proc. R. Soc. Lond. B* **264**, 1317–1324.
- Price, J., Droegge, S. & Price, A. 1995 *The summer atlas of North American birds*. London: Academic Press.
- Price, T. & Liou, L. 1989 Selection on clutch size in birds. *Am. Nat.* **134**, 950–959.
- Robertson, R. J., Stutchbury, B. J. & Cohen, R. R. 1992 Tree swallow. In *The birds of North America*, vol. 11 (ed. A. Poole, P. Stettenheim & F. Gill), 28 pp. Philadelphia, PA: Academy of Natural Sciences; and Washington: American Ornithologists' Union.
- Robins, J. D. 1970 The relationship of food supply to the timing of breeding in aerial foragers. *Kansas Ornithol. Soc. Bull.* **21**, 9–15.
- Roeder, K. D. 1953 *Insect physiology*. New York: Wiley.
- Root, T. 1988 *Atlas of wintering North American birds*. University of Chicago Press.
- Visser, M. E., Van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. 1998 Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. R. Soc. Lond. B* **265**, 1867–1870.
- Wilkinson, L. 1992 *Systat: graphics, version 5.2*. Evanston, IL: Systat, Inc.
- Winkel, W. & Hudde, H. 1997 Long-term trends in reproductive traits of tits (*Parus major*, *P. caeruleus*) and pied flycatchers *Ficedula hypoleuca*. *J. Avian Biol.* **28**, 187–190.
- Winkler, D. W. & Allen, P. E. 1996 The seasonal decline in tree swallow clutch size: physiological constraint or strategic adjustment? *Ecology* **77**, 922–932.